

## RESEARCH ARTICLE

## Dynamics of invertebrate communities on the stony littoral of the Neva Estuary (Baltic Sea) under macroalgal blooms and bioinvasions

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### Abstract

- 1 - The Littoral zone of the Neva Estuary is strongly influenced by “macroalgal blooms” (mainly *Cladophora glomerata*). The present paper aims to study species composition, abundance and seasonal dynamics of littoral invertebrate communities in the Neva Estuary in order to assess their current status and the influence of macroalgal blooms on invertebrates.
- 2 - Littoral communities at three sites in the Neva Estuary were monitored during May to October of 2002, 2004 and 2005. Quantitative sampling of macroinvertebrates at a depth of 0.5 m was carried out with a 0.03 m<sup>2</sup> cylindrical metal frame. Temperature, conductivity, dissolved oxygen and total phosphorus in water were measured at studied sites using a WTW Oxi330 oxygen meter, a DistWP4 conductivity meter and standard analytic techniques.
- 3 - A list of macroinvertebrate species includes 104 taxa in the freshwater part of the Neva Estuary and considerably fewer in its oligohaline part due to the disappearance of some species of typical freshwater groups (oligochaetes and dipterans). Amphipods *Gmelinoides fasciatus* and *Pontogammarus robustoides*, recent invaders to the Neva Estuary, were abundant species at all studied habitats of the estuary, accounting for 73 % of the total biomass of zoobenthos.
- 4 - We obtained significant positive correlations between the density of invertebrate groups (oligochaetes, chironomids, ephemeropterans, trichopterans, amphipods) and oxygen content in water. Temporary hypoxia (0.62–2.8 mg l<sup>-1</sup>) and a 4-10-fold decrease in the density of amphipods, oligochaetes and aquatic insects were recorded in littoral habitats during decomposition of drifting filamentous algae (July-August). We conclude that intensive macroalgal blooms in the littoral zone due to the intense eutrophication of the Neva Estuary can negatively affect the density of intolerant species and groups and the structure of the invertebrate community through deterioration of oxygen conditions and increase of nutrients during intensive decomposition of drifting algae.

**Keywords:** macroinvertebrates, littoral community, species composition, abundance, eutrophication, macroalgal blooms, introduced species.

### Introduction

The Neva Estuary is one of the largest estuaries in the Baltic Sea, consisting of three main parts: the Neva Bay (400 km<sup>2</sup>) and the inner and outer estuary (3,200 km<sup>2</sup>). Neva Bay is the freshwater part, separated from the other parts of the estuary by a storm-surge barrier since the early

1980s (Fig. 1). The storm-surge barrier has several sluices in the northern part and a broad ship gate in the southern part of the estuary. The Gulf of Finland, including the Neva Estuary, is known to be one of the most eutrophic areas of the Baltic Sea (Lappäläinen, Ponni, 2000), annually receiving 7.6 thousand tons of

phosphorus and 138 thousand tons of nitrogen (Pitkänen *et al.*, 1998). The estuary is impacted by a number of human activities such as discharges of large amounts of waste waters from Sankt-Petersburg and its province, intensive ship traffic, development of new ports and oil terminals, commercial fisheries and recreation.

The littoral zone of the Neva Estuary is dominated by macrophytes proliferating on hard substrates, which together with their epiphytes provide large amounts of organic matter. Increased nutrient inputs from point sources in the Neva River and the upper estuary have stimulated the growth of fast-growing filamentous algae (mainly a green alga *Cladophora glomerata*). The production of *C. glomerata* has been put at 7 g Cm<sup>-2</sup> per day, or 800-900 g Cm<sup>-2</sup> per vegetation period, which is at least twice the production of phytoplankton in the open waters of the Neva Estuary (Berezina *et al.*, 2005). This value is similar to the production of rocky shore ecosystems along the Atlantic coasts of Europe and other parts of the Baltic (Bird, Benson, 1987; Bokn *et al.*, 2002). The high primary production of the littoral zone of the Neva Estuary supports complex and highly productive invertebrate communities, including annelids, amphipods, isopods, mussels and aquatic insects that feed on the produced algal matter (Alimov, 1988, Berezina, Panov, 2003, Golubkov *et al.*, 2003 a, 2003 b).

Unfavourable conditions in the littoral zone of the Neva Estuary appear to be the consequence of large *Cladophora* "blooms", storm activity and fluctuations in the water level induced by the wind, seiches and changes in the Neva River runoff. These phenomena become more frequent around the middle of summer, dramatically affecting the growth of filamentous algae, detaching them from their hard substrates. Great masses of the algae drift into the shallow littoral zone, forming loose-lying algal mats or accumulating on beaches. Occupying different habitats, the drifting algae mats represent a serious threat to the biodiversity of coastal areas (Norkko, Bonsdorff, 1996 a, 1996 b).

The present study focuses on species composition, abundance and seasonal dynamics

of littoral invertebrate communities in the Neva estuary in order to assess the current status of invertebrate communities in the littoral ecosystem and clarify whether macroalgal blooms influence negatively the communities in the study area.

## Methods

From May to October dynamics of littoral communities were studied at three sites at a depth of 0.5 m at two-week intervals in 2002 and 2004 and monthly in 2005. Species composition, density and the biomass of macroinvertebrate communities were obtained during the intensive surveys. During the sampling, the temperature, dissolved oxygen, total phosphorus and conductivity of the water were also measured.

Quantitative samples of macroinvertebrates at a depth 0.5 m were gathered with a 0.03 m<sup>2</sup> cylindrical metal frame 0.7 m in height in accordance with a previously proposed approach (Berezina *et al.*, 2005). All samples were taken in three replicates. The samples were preserved in 4 % formaldehyde and transported to the laboratory in plastic bags. In the laboratory, all invertebrates longer than 2 mm (macroinvertebrates) were handpicked. In addition, macroalgae were picked from each sample, rinsed with tap water, dried (at 60 °C for 96 h) and weighed. The density and biomass of invertebrates were measured as the mean value of all replicates and then re-calculated for 1 m<sup>2</sup> of sea bed. Measurements of temperature and oxygen content in water were conducted with a WTW Oxi 330 oxygen meter. Conductivity (E, µS) was measured with a DistWP4 conductivity meter at 25 °C. Total dissolved salt concentration (TDS, mg l<sup>-1</sup>) in water was re-calculated from conductivity using the formula:  $TDS = 0.47 \cdot E^{1.08}$ . To get total phosphorus concentration (P), the 100-ml samples of water were hydrolyzed with H<sub>2</sub>SO<sub>4</sub> according to standard techniques (Golterman, 1969). The measured biological characteristics were expressed as the mean value ± SE (standard error). Possible differences in densities and biomasses between sites and years

were analysed by ANOVA. Pearson's correlation coefficient was used to test the

relationships between characteristics of key zoobenthic groups and oxygen content.

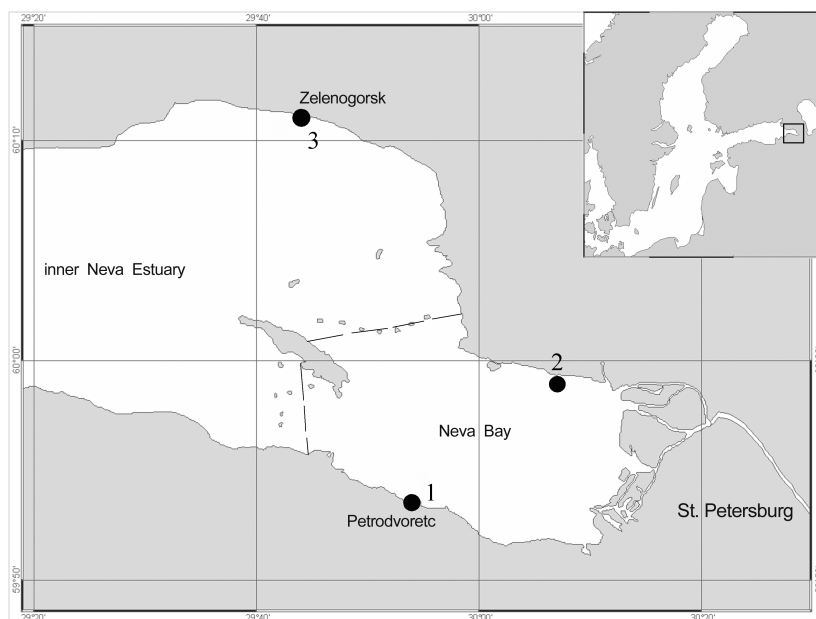


Figure 1. Map of the Neva Estuary with sampling sites. Site 1 – Petrodvorets park, site 2 – Olgino city, site 3 – Zelenogorsk city (Resort District).

## Results

### Habitat conditions

Table 1 summarizes the results for total dissolved salt content and total phosphorus concentration in the water. The lowest salt content ( $42\text{--}75\text{ mg l}^{-1}$ ) was recorded at site 2 due to the strong influence of the Neva River, the major tributary to the eastern Gulf of Finland. Water salinity increased considerably outside the dam in the inner estuary, mixing with mesohaline waters from the open Gulf of Finland. At site 3 TDS often exceeded  $1000\text{ mg l}^{-1}$ . Total phosphorus concentration ranged from  $23\text{--}110\text{ }\mu\text{g l}^{-1}$  and  $36\text{--}160\text{ }\mu\text{g l}^{-1}$  in the northern and southern Neva Bay respectively. At site 3 this parameter ranged widely, reaching a maximum of  $340\text{ }\mu\text{g l}^{-1}$ . All the studied sites can be characterized as “eutrophic zones” with nutrient-rich water.

As a rule, in the eastern Gulf of Finland during December to March, the water temperature is close to  $0^\circ\text{C}$ . The temperature rapidly increases after the ice-breaking in April-May. The period with temperatures above  $10^\circ\text{C}$  lasts around 120 days (Savchuk, Davidan 1997). Figure 2 outlines the temperature regime of waters in the

littoral zone during the sampling period. By May, the water temperature reached  $9\text{--}11^\circ\text{C}$ . The summer daytime temperature varied in the range of  $18\text{--}23^\circ\text{C}$  in 2002,  $14\text{--}25^\circ\text{C}$  in 2004 and  $16\text{--}25^\circ\text{C}$  in 2005. In September the temperature decreased to  $8\text{--}14^\circ\text{C}$ . At the end of October it dropped below  $3^\circ\text{C}$ .

The substrate at the studied locations consists of coarse sand, gravel and stones. Projective coverage of the bottom by hard substrates averages 60% at site 1, 90% at site 2 and 20% at site 3. In different part of the Neva Estuary, macroalgal communities developing on hard substrates consist of green algae *Cladophora glomerata* (L.), *Enteromorpha intestinalis* (L.), brown algae *Pilayella littoralis* (L.), *Ectocarpus* sp. and a red alga *Ceramium rubrum* (Hudson). At the study sites, the communities include mainly a green alga *C. glomerata* proliferating from late May to late September on hard substrates. Macrophyte beds representing mainly *Potamogeton* spp. developed during July to September. The biomass of filamentous algae varied between sites and years, averaging in the range of  $13.9$  to  $76.1\text{ gm}^{-2}$  dry weight (Table 1). It tended to higher growth in the northern inner Neva Estuary (sites 2 and 3).

Table 1. Coordinates, salinity, phosphorus concentration and biomass of filamentous algae (as dry weight) at study sites in the Neva Estuary during sampling period

	Site	1 59°53' N, 29°54' E	2 59°59' N, 30°05' E	3 60°11' N, 29°44' E
Total dissolved salts (g l <sup>-1</sup> )	2002	0.24-0.38	0.05-0.07	0.40-1.08
	2004	0.20-0.48	0.05-0.06	0.38-0.93
	2005	0.29-0.56	0.04-0.07	0.63-1.4
Total phosphorus, µg l <sup>-1</sup>	2002	36-88	30-80	64-114
	2004	84-160	23-110	44-260
	2005	88-140	20-110	65-340
Biomass of algae, gDW m <sup>-2</sup>	2002	18.8±11.3	24.5±11.9	35.7±10.3
	2004	51.7±11.6	76.1±51.2	42.1±6.8
	2005	14.35±10.9	22.4±12.6	13.9±8.1

Daytime dissolved oxygen levels, arising from photosynthesis of aquatic plants and from the



Figure 2. Dynamics of temperature during observation period in the littoral zone of the Neva Estuary

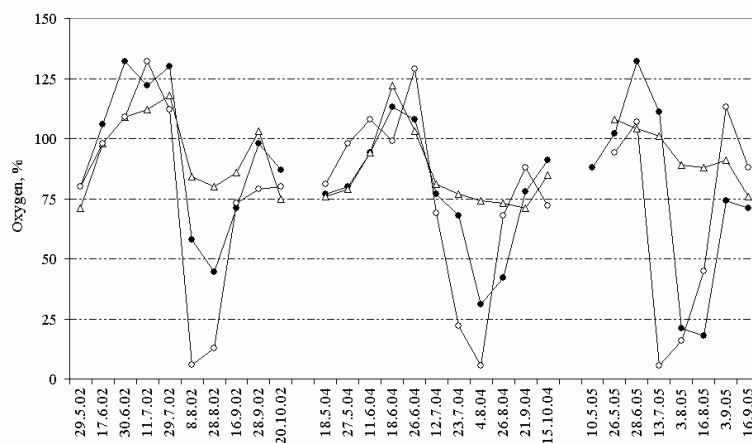


Figure 3. Dynamics of oxygen saturation (%) in water at studied sites during sampling period.

### Species composition of the invertebrate community in the littoral zone

The richness of macroinvertebrate species in the littoral communities was high. The list of benthic species includes 116 taxa (Table 2). The highest numbers of species (and group of species) were found for oligochaetes (41) and

air-water interface, ranged from 68–132% at all studied sites during most of the observation period. However, temporary falls in oxygen concentration were recorded during decomposition of drifting filamentous algae in August of 2004 and 2005 at site 1, and in July of 2004 and in August of all years at site 3 (Fig. 3). During these periods the dissolved oxygen content in water near the bottom reached 5.4–31 % or 0.62–2.8 mg l<sup>-1</sup>.

chironomids (34). Three amphipod species, *Gmelinoides fasciatus*, *Pontogammarus robustoides* and *Chaetogammarus warpachowskyi* and the mollusc *Dreissena polymorpha* on this list are introduced species. In the freshwater Neva Bay, the number of recorded species reached 104. In the oligohaline

part of the estuary (site 3) more than 20 % of typical freshwater species disappeared from the community and although some species of oligohaline organisms (amphipods, molluscs and others) were added to the fauna list, the species richness significantly decreased (to 70).

### Relative abundance of different species and groups in total biomass

Average absolute and relative biomasses of invertebrates differed significantly between taxonomic groups ( $F = 3.45$ ,  $p < 0.001$ ) and study sites ( $F = 3.64$ ,  $p = 0.034$ ). At sites 1 and 2, the introduced amphipod species accounted for most of the total biomass, ranging from 44

to 73 % (Fig. 4). At site 1 in Neva Bay *G. fasciatus* and *P. robustoides* reached the maximum biomass ( $13.2 \text{ gm}^{-2}$  and  $24.8 \text{ gm}^{-2}$ , respectively) in the summer of 2004. At site 3 their relative abundance was significantly lower, varying from 8 to 36 % in different years. Chironomids, oligochaetes, molluscs, ephemeropterans and hirudineans were also common in the community, with high relative abundances ( $> 7 \%$ ). Oligochaetes comprised up to 30 % of total biomass at site 1. Molluscs and hirudineans were dominant groups at site 2, reaching 22 and 15%, respectively. The relative biomass of chironomids reached a maximum of 48 % at site 3.

Table 2. Species list of macroinvertebrates in the littoral zone of the Neva Estuary

Group, species name	Site 1	Site 2	Site 3
Class: Aphanoneura			
Aeolosomatidae			
<i>Aeolosoma</i> sp.	+	+	
Class: Clitellata			
Oligochaeta			
Naididae			
<i>Stylaria lacustris</i> (L)	+	+	+
<i>Vejdovskyella intermedia</i> (Bretscher)	+		
<i>Slavina appendiculata</i> (Udekem)		+	
<i>Piguetiella blanci</i> (Piguet)		+	
<i>Nais barbata</i> Muller	+	+	+
<i>N. behningi</i> Michaelsen		+	
<i>N. bretscheri</i> Michaelsen	+	+	
<i>N. christinae</i> Kasprzak	+		
<i>N. communis</i> Piguet	+	+	+
<i>N. elinguis</i> Muller	+		+
<i>N. pardalis</i> Piguet	+	+	+
<i>N. pseudobtusa</i> Piguet		+	
<i>N. variabilis</i> Piguet		+	+
<i>Specaria josinae</i> (Vejdovsky)	+	+	
<i>Uncinais uncinata</i> (Oersted)	+	+	+
<i>Paranaïs botniensis</i> Sperber	+		+
<i>P. litoralis</i> (Muller)	+		+
<i>Amphicyaeta leydigi</i> Tauber	+	+	+
<i>A. sannio</i> Kallstenius	+		
<i>Chaetogaster diaphanus</i> (Gruithuisen)	+	+	+
<i>C. diastrophus</i> (Gruithuisen)	+	+	+
<i>C. langi</i> Bretscher	+		
<i>Pristina foreli</i> Piguet	+	+	+
<i>Pristinella bilobata</i> (Bretscher)	+	+	+
<i>P. rosea</i> (Piguet)	+		
Tubificidae			
<i>Rhyacodrilus</i> sp.	+	+	
<i>Aulodrilus limnobius</i> Bretscher		+	

<i>Tubifex tubifex</i> (Muller)	+	+	
<i>Spirosperma ferox</i> Eisen		+	+
<i>Limnodrilus claparedeanus</i> Ratzel	+	+	
<i>L. hoffmeisteri</i> Claparede	+	+	+
<i>L. profundicula</i> (Verrill)	+	+	+
<i>Tubificidae</i> genus sp.	+	+	+
<i>Tubifex tubifex</i> (Muller)	+	+	
<i>Tubificidae</i> genus sp.	+	+	+
Enchytraeidae			
<i>Cernosvitoviella</i> sp.		+	
<i>Cognettia glandulosa</i> (Michaelsen)		+	

Table 2. (cont.)

Group, species name	Site 1	Site 2	Site 3
<i>Lumbricillus lineatus</i> (Muller)	+	+	+
<i>Henlea</i> sp.	+		+
<i>Enchytraeidae</i> genus sp.	+	+	+
Hirudinea			
<i>Helobdella stagnalis</i> (L)	+	+	
<i>Erpobdella octoculata</i> (L)	+	+	+
<i>Glossiphonia complanata</i> (L)	+	+	+
Class: Crustacea			
Amphipoda			
<i>Chaetogammarus warpachowskyi</i> (Sars)			+
<i>Gammarus inaequicauda</i> Stock			+
<i>G. pulex</i> (L)	+		
<i>G. zaddachi</i> Sexton			+
<i>Gmelinoides fasciatus</i> (Stebbing)	+	+	+
<i>Pontogammarus robustoides</i> (Sars)	+		+
Mysidae			
<i>Neomysis integer</i> (Leach)			+
Isopoda			
<i>Asellus aquaticus</i> (L)	+	+	+
Class: Mollusca			
Bivalvia			
<i>Dreissena polymorpha</i> Pallas			+
<i>Pisidium inflatum</i> (Muehlfeld in Poro)	+	+	
<i>Anadonta</i> sp.	+	+	+
<i>Sphaerium corneum</i> (L)	+	+	
<i>Musculium lacustre</i> Mueller		+	
<i>Euglesa</i> spp.	+	+	+
Gastropoda			
<i>Anisus vortex</i> (L)		+	+
<i>Bythinia tentaculata</i> (L)	+		+
<i>Lymnaea glutinosa</i> (Mueller)	+	+	
<i>L. ovata</i> (Draparnaud)	+	+	+
<i>Planorbis planorbis</i> (L)	+		+
<i>Teodoxus fluviatilis</i> (L)			+
<i>Valvata</i> sp.	+		
<i>Viviparus viviparus</i> (L)	+	+	
Class: Insecta			
Ephemeroptera			
<i>Caenis undosa</i> Tiensuu	+	+	+
<i>Ephemerella ignita</i> Poda	+		+
<i>Ephoron virgo</i> (Oliv)	+	+	+

<i>Baetidae</i> gen sp.	+	+	
<i>Siphonurus lacustris</i> (Eaton)	+	+	
<i>Eurylophella mucronata</i> Bengtsson		+	
<i>Potamanthus luteus</i> L		+	
Trichoptera			
<i>Agraylea multipunctata</i> Curt	+	+	+
<i>Athripsodes cinereus</i> Curt	+	+	
<i>Hydropsyche contubernalis</i> MacLachlan	+	+	+
<i>Holocentropus stagnalis</i> Albarda	+	+	
<i>Limnephilus</i> sp.		+	

Table 2. (cont.)

Group, species name	Site 1	Site 2	Site 3
Lepidoptera			
<i>Parapoynx stratiotata</i> L	+	+	
Coleoptera			
<i>Haliphus</i> sp.	+	+	+
Megaloptera			
<i>Sialis</i> sp.	+		+
Diptera			
Chironomidae			
Chironominae			
<i>Chironomus</i> sp.	+	+	+
<i>Cladotanytarsus</i> gr. <i>mancus</i>	+	+	+
<i>Cryptochironomus</i> gr. <i>defectus</i>	+	+	+
<i>Einfeldia carbonaria</i> (Meigen)	+		
<i>Einfeldia</i> sp.		+	+
<i>Endochironomus stakelbergi</i> Goetghebuer	+	+	+
<i>Glyptotendipes barbipes</i> (Staeger)	+		
<i>G. glaucus</i> (Meigen)	+		+
<i>G. gripekoveni</i> (Kieffer)	+		+
<i>G. paripes</i> (Edwards)	+		
<i>Microtendipes</i> gr. <i>pedellus</i>	+	+	+
<i>Paratanytarsus austriacus</i> (Kieffer)		+	+
<i>Paratendipes</i> gr. <i>albimanus</i>	+		
<i>Polypedilum</i> gr. <i>nubeculosum</i>		+	+
<i>Pseudochironomus prasinatus</i> (Staeger)			+
<i>Stictochironomus crassiforceps</i> (Kieffer)			+
<i>Tanytarsus pallidicornis</i> (Walker)	+		
<i>T. verralli</i> Goetghebuer	+	+	+
Orthoclaadiinae			
<i>Abiskomyia</i> sp.	+		
<i>Corynoneura</i> sp.	+	+	+
<i>Cricotopus</i> gr. <i>festivellus</i>	+	+	+
<i>C. gr. intersektus</i>	+	+	+
<i>C. gr. reversus</i>	+	+	
<i>C. gr. sylvestris</i>			+
<i>C. gr. tremulus</i>	+		
<i>Cricotopus</i> sp.	+	+	+
<i>Paratrihocladius</i> sp.	+		
<i>Psectrocladius barbimanus</i> (Edwards)	+		+
<i>Psectrocladius bisetus</i> (Goetghebuer)	+		+
<i>Psectrocladius sordidellus</i> (Zetterstedt)			+
<i>Psectrocladius</i> sp.	+		+

<i>Synorthocladus semivirens</i> (Kieffer)			+
Tanypodinae			+
<i>Ablabesmyia</i> sp.			+
Diamesinae			
<i>Diamesa</i> sp.		+	+
Ceratopogonidae			
<i>Serromyia</i> sp.		+	

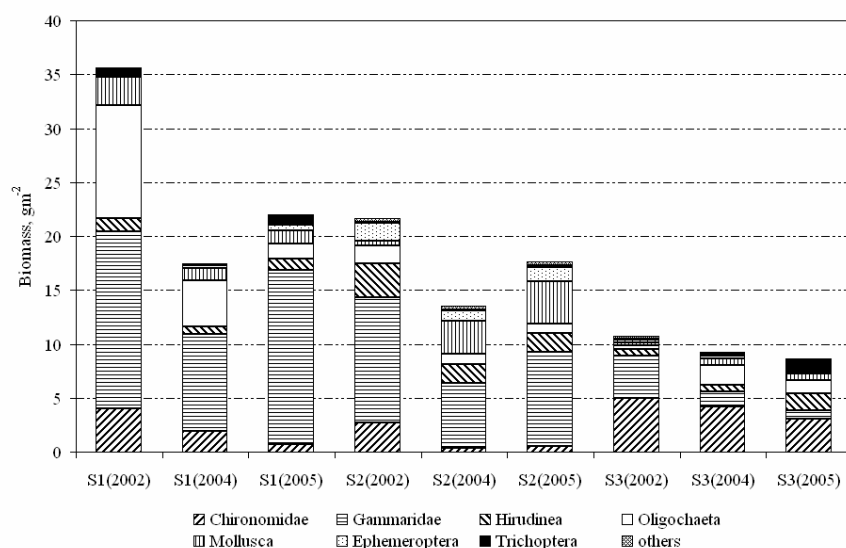


Figure 4. Average biomass (mean for each season) of different invertebrate groups at study sites in the Neva Estuary.

## Discussion

The present study showed that deoxygenation of water during decomposition of drifting macroalgae influences macroinvertebrate communities, resulting in a decrease in density of invertebrate groups and structural changes. Decomposition of macroalgae causes periodical hypoxic conditions in the littoral zone of the Neva Estuary during late July-August. Excessive growth of opportunistic macroalgae, called “macroalgal blooms”, has become a widely-observed phenomenon in different parts of the Baltic Sea, constituting a major nuisance in shallow coastal zones (Blomster *et al.*, 2002, Paalme *et al.*, 2002, Cummis *et al.*, 2004, Kotwicki *et al.*, 2005, Lauringson, Kotta, 2006). The algal mats form in shallow areas and may later accumulate in deeper zones, covering an area of several hectares (Valiela *et al.*, 1997). It was shown that decomposition of the drifting mats causes modification of nutrient dynamics in the water column and sediments, results in widespread hypoxic and anoxic conditions in

littoral habitats and negatively affects communities of invertebrates, seagrass beds and feeding by wading birds (Norkko & Bonsdorff, 1996 a, 1996 b; Peckol, Riviers, 1996; Raffaelli *et al.*, 1998; Lehvo, Bäck, 2001; Berglund *et al.*, 2003). Decaying macroalgal mats generate low oxygen conditions in the inter-algal water (0–1 mg l<sup>-1</sup>), corresponding to zones of high and relatively stable phosphate and ammonium concentrations (up to 96 µg l<sup>-1</sup> and 166 µg l<sup>-1</sup>, respectively). In addition, this process may often be accompanied by the release of toxic hydrogen sulphide (Lavery, McComb 1991).

As is known, the algal mats can substantially modify nutrient dynamics in the water column and sediments. Large amounts of tissue phosphorus (to 65 %) are released by decaying mats of *C. glomerata* during the decomposition process (Paalme *et al.*, 2002). In photosynthetically inactive portions of the algal mats, annual carbon release was estimated from tissue-loss measurements for *Cladophora*



*vagabunda*. It is around 20% of annual net mat production (Peckol, Rivers, 1996).

Rapid decomposition provides an additional supply of organic and inorganic compounds to be potentially recycled in the water, increasing eutrophication. At the same time, the increase in nutrients due to the decomposition of drifting and loose-lying algal mats is not likely to have a direct influence on the density and structure of macroinvertebrate communities. In some mesocosms, experiments have shown that the

majority of invertebrate groups change only slightly in response to nutrient treatment, but a significant increase in the density of the common periwinkle *Littorina littorea* in response to nutrient loading has been observed (Kraufvelin *et al.*, 2002).

Our results show that an abrupt decline in the density of many invertebrate groups coincided with oxygen deficiency in the water during periods of decaying algae decomposition, confirmed by the correlation analysis.

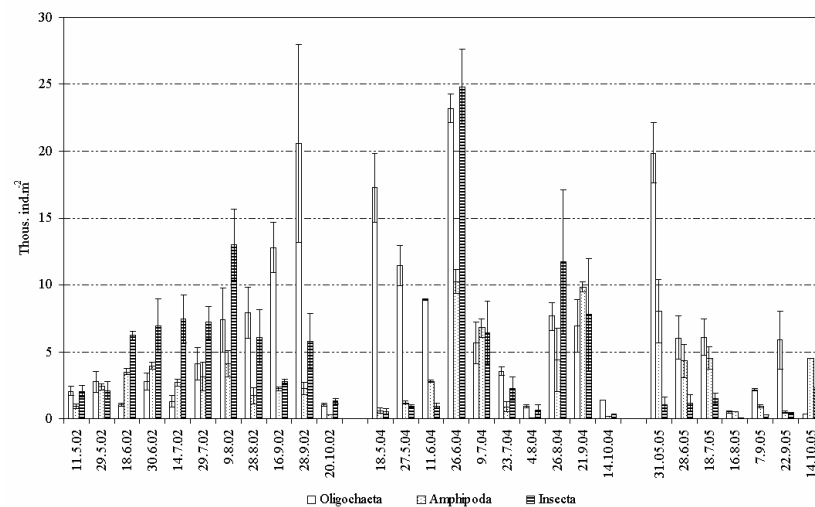


Figure 5. Dynamics of abundant invertebrate groups (oligochaetes, amphipods and insects) at site 1 in the Neva Estuary.

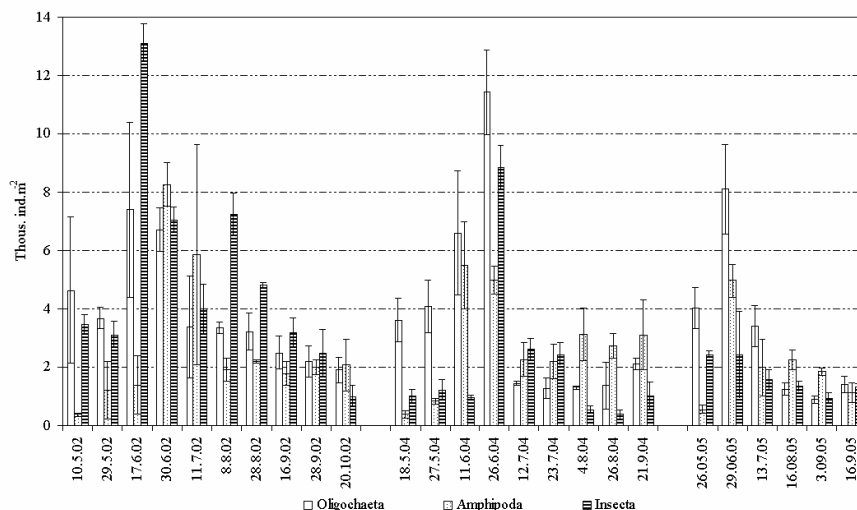


Figure 6. Dynamics of abundant invertebrate groups (oligochaetes, amphipods and insects) at site 2 in the Neva Estuary

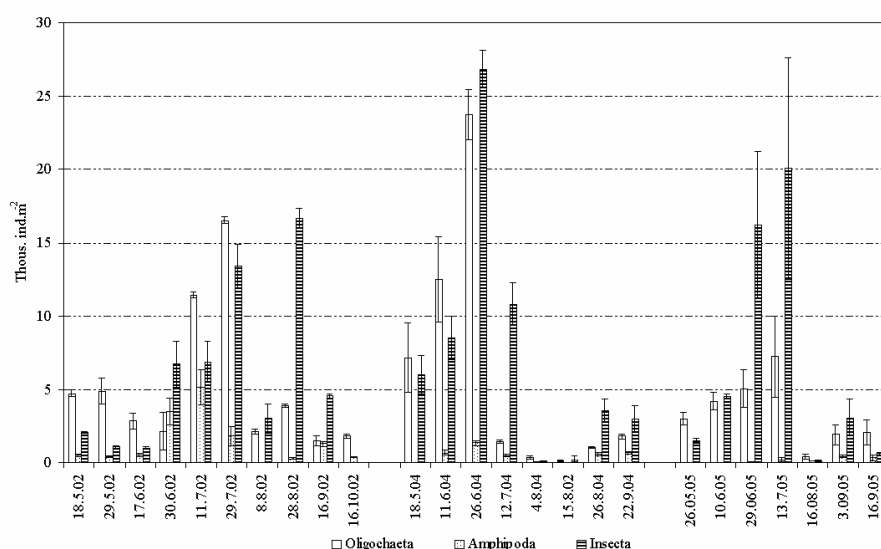


Figure 7. Dynamics of abundant invertebrate groups (oligochaetes, amphipods and insects) at site 3 in the Neva Estuary.

The decline in density is a result of migration of mobile invertebrates and/or large-scale death of many invertebrates under low oxygen conditions which occurred below the critical threshold of their survival. Survival of many invertebrates (amphipods and aquatic insects) is limited in nature by oxygen concentration in water around  $2 \text{ mg l}^{-1}$ . It may decrease sharply under hypoxic conditions in the shallow zone of the Neva Estuary. Experimentally measured lethal concentrations of oxygen at  $20^\circ\text{C}$  were  $0.5 \text{ mg OI}^{-1}$  for amphipod *G. fasciatus* and  $0.3\text{--}0.4 \text{ mg OI}^{-1}$  for amphipod *P. robustoides* (Berezina et al., 2005).

The high density of different groups of invertebrates including introduced amphipods *P. robustoides* and *G. fasciatus* in the littoral zone of the Neva Estuary excluding the periods of temporarily lower oxygen content testify to the favourable food conditions in the studied habitats. We also assume that the high biomass of introduced amphipods might be one of possible causes of low biomass of chironomids in some locations of the Neva Estuary, as was observed at sites 1 and 2. Similar phenomena have been recorded in other studies (Kelly et al., 2003; Kelly, Dick 2005 a, 2005 b, Orlova et al., 2006), when introduced amphipods dramatically altered invertebrate communities (mainly aquatic insects) and fish through strong

predatory and competitive interactions. However, disturbance factors such as eutrophication, macroalgal blooms and oxygen deficiency may facilitate the success of opportunistic species including the introduced amphipod and the alterations in macroinvertebrate communities. In many cases it is difficult to determine if the changes in a community are due solely to the effects of the invader or other factors. In the case of Neva Estuary we conclude that macroalgal blooms resulting in deoxygenation of bottom habitats is the main environmental reason for changes in the structure and dynamics of invertebrate communities.

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